

DEVELOPMENT OF THE DIMORPHIC CLAW CLOSER MUSCLES OF THE LOBSTER *HOMARUS AMERICANUS*. III. TRANSFORMATION TO DIMORPHIC MUSCLES IN JUVENILES

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The asymmetry observed in the chelipeds of many crustaceans presents interesting problems in a number of areas, including development, behavior, and neuromuscular physiology. While asymmetry is fixed in some animals (Przibram, 1931), there are a number of examples where it has been demonstrated that claw type can be "reversed." That is, loss of one claw, usually the larger or "crusher" will result in transformation of the remaining smaller claw, the "cutter," into a crusher. The regenerated claw will then become a cutter (Przibram, 1931; Hamilton, Nishimoto, and Halusky, 1976). Furthermore, in some of the species in which reversal has been demonstrated, it has also been shown that the claws are used for different behaviors (e.g., *Alpheus*, Przibram, 1931; *Calappa*, Shoup, 1968; Lewis, 1969; *Callinectes*, Hamilton *et al.*, 1976). Thus, it would be of interest to ascertain the mechanisms underlying both the morphogenetic changes which are manifested and also the possible central nervous system modifications which in some cases must also occur. There presently is little information regarding the neuromuscular physiology or development of any of the aforementioned crustaceans, either before or after reversal. Ritzman (1974) has described the neural mechanisms underlying closure of the large snapping claw in two species of *Alpheus*, but has not reported similar studies for the smaller "pinch-claw" or after claw reversal. While it is not yet known whether the muscle fiber populations differ between the two claws, they are certainly used differently in the behavioral repertoires of the animals (Darby, 1934). Thus the pinch-claw is not merely a miniature snapping claw which hypertrophies upon loss of the snapping claw.

Warner and Jones (1976) have studied muscle fiber properties in the dimorphic claws of *Macrohippus depurator*. Although the stouter chela of this animal has a higher mechanical advantage than the smaller chela, there was no consistent difference between the muscle fiber populations found in each claw; both claws contained "slow" type fibers with sarcomere lengths of 6-10 μm .

In adult lobsters (*Homarus americanus*) the dimorphic claws contain closer muscles which have different populations of muscle fiber types (Jahromi and Attwood, 1971; Goudey and Lang, 1974). The fast acting cutter claw closer muscle is composed of over 60% short sarcomere (2-4 μm), fast fibers with the remainder being long sarcomere (6-12 μm), slow fibers. The slow acting crusher closer muscle has virtually all long sarcomere (>6 μm), slow fibers. Furthermore, in the cutter muscle, fast and slow fibers are regionally distributed on the inner aspect with fast fibers in the dorsal and central medial sections and slow fibers in the ventral sections (Lang, Costello, and Govind, 1977).

In larval lobsters the claws are identical and, indeed, the paired closer muscles have not differentiated into cutter and crusher types. In fact, the muscles are symmetrical in early larval animals (stages 1-2), being composed of 30-40% short sarcomere, over 50% intermediate and only 10% long sarcomere fibers. In the late larval lobsters (stage 3) there is a nearly equal distribution of short, intermediate and long sarcomere fibers (Lang, Govind and She, 1977). Thus, the transformation of the paired symmetrical muscles into cutter and crusher types must occur in postlarval (juvenile) forms.

In the larval stages (1-3) and early juvenile stages (4 and 5) the two claws are identical in external appearance, both being cutter-like (Herrick, 1896, 1911). A distinct change in external morphology of the paired claws into cutter and crusher claws is seen only at stage 7 or 8 when the cutter has a longer, more slender shape and the crusher has a larger blunt tooth (Herrick, 1896). It is reasonable to assume that the transformation in external character signals muscle fiber differentiation in the closer muscle. Muscle fiber types and their distribution in several juvenile stages were examined in this study and, while differentiation of the cutter muscle occurs as early as stage 6, that of the crusher is not usually completed until at least stage 13.

MATERIALS AND METHODS

Newly hatched larval lobsters were obtained from the Massachusetts State Hatchery on Martha's Vineyard and reared in running seawater tanks at 20-23° C according to the methods of Hughes, Shleser and Tchobanoglous (1974). Their early development consists of three pelagic mysis (larval) stages. When they molt to the fourth stage they approximate their adult form, and during this stage, or the following one, they assume a benthic existence (Herrick, 1896). From the fourth stage onward, the juvenile lobsters were reared in individual trays (Lang, 1975) and their growth followed for periods up to two years.

Several animals were examined in the early or late period of the molting cycle. In the former case, animals were used within one or two days after a molt. In the latter case, two criteria were used to establish that lobsters were in the late part of the stage, *i.e.*, about to molt: first, when molting had occurred in animals that had simultaneously entered the same stage and had been kept under similar conditions; and secondly, the typical premolting behavior of failing to eat food put into the tray.

The claw closer muscles were fixed with Bouin's solution while the daetyl was in the fully open position. Methods for isolating muscle fibers and measuring sarcomere lengths have been previously described (Lang, Costello and Govind, 1977). The average sarcomere length for a fiber was established by measuring five consecutive sarcomeres in three separate myofibril bundles. Sarcomeres were sampled from the inner aspect of the closer muscle which was subdivided into nine sections. This partitioned the muscle laterally into dorsal, medial and ventral sections, and transversely into proximal, central and distal sections (Lang, Costello, and Govind, 1977). For some stage 4 animals the muscle was divided into only six sections by omitting a medial section and retaining only the dorsal and ventral sections. In most animals, ten fibers were inspected in each section giving a total sample of 90 fibers for each muscle; in four stage 4 animals, only 60 fibers were sampled from

the six sections for each muscle. It is estimated that each closer muscle contains 600–700 fibers; thus we are sampling approximately 13–15% of the total population. However, the extremely small size of the closer muscle may well have introduced significant errors in the sampling procedure. In a fourth stage animal, this muscle is 1.5 mm in length. Thus each sampling area is quite small, and there undoubtedly was some heterogeneity of the fiber population sampled for a given area. For this reason, the statistical test (Kolmogorov-Smirnov two-sample test) was employed as a guide rather than the sole criterion for determining differences between sampled muscles.

RESULTS

Herrick (1896) reported that the paired claws are symmetrical in external morphology in the first three juvenile (postlarval) stages (*i.e.*, stages 4 to 6) and subsequently differentiate into crusher and cutter claws from stage 7 or 8 onward. In stage 6 lobsters, one dactyl is always slightly longer than the other and is thus destined to be the cutter claw dactyl. By careful measurement, claw type in stage 6 could be unequivocally determined. Therefore, the first three juvenile forms, *i.e.*, stages 4, 5, and 6 and several later stages, namely, stages 11, 13, and 15, were examined. The results are summarized in Table I, in which the paired closer

TABLE I

Distribution of muscle fiber types in the paired claw closer muscles of juvenile lobsters.

Stage	Length of animal (rostrum to telson, cm)	Muscle fiber type based on sarcomere length (μm)					
		Claw I/Cutter			Claw II/Crusher		
		Short 4	Intermediate 4–6	Long 6	Short 4	Intermediate 4–6	Long 6
4 (early)*	1.2	35%	13%	52%	32%	15%	53%
4 (early)*	1.2	27	8	65	27	3	70
4*	1.25	35	3	62	17	3	80
4*	1.25	45	8	47	32	0	68
4	1.2	44	0	56	22	0	78
4	1.2	43	2	55	32	0	68
4	1.3	24	0	76	19	2	79
5 (early)	1.4	47	1	52	27	1	72
5	1.4	37	0	63	30	1	69
5 (late)	1.5	67	2	31	24	0	76**
6 (early)	1.5	59	0	41	18	0	82**
6	1.65	64	1	35	32	0	68**
6	1.7	58	0	42	6	2	92**
6	1.7	41	0	59	27	0	73
11	3.2	67	1	32	11	0	89**
11	3.3	79	0	21	34	2	64**
13	3.9	64	0	36	0	0	100**
15	5.5	82	0	18	4	0	96**

* Sixty muscle fibers sampled from each closer muscle; in all other animals, 90 fibers were sampled in each muscle.

** Closer muscles significantly different at 0.01 level (Kolmogorov-Smirnov two-sample test).

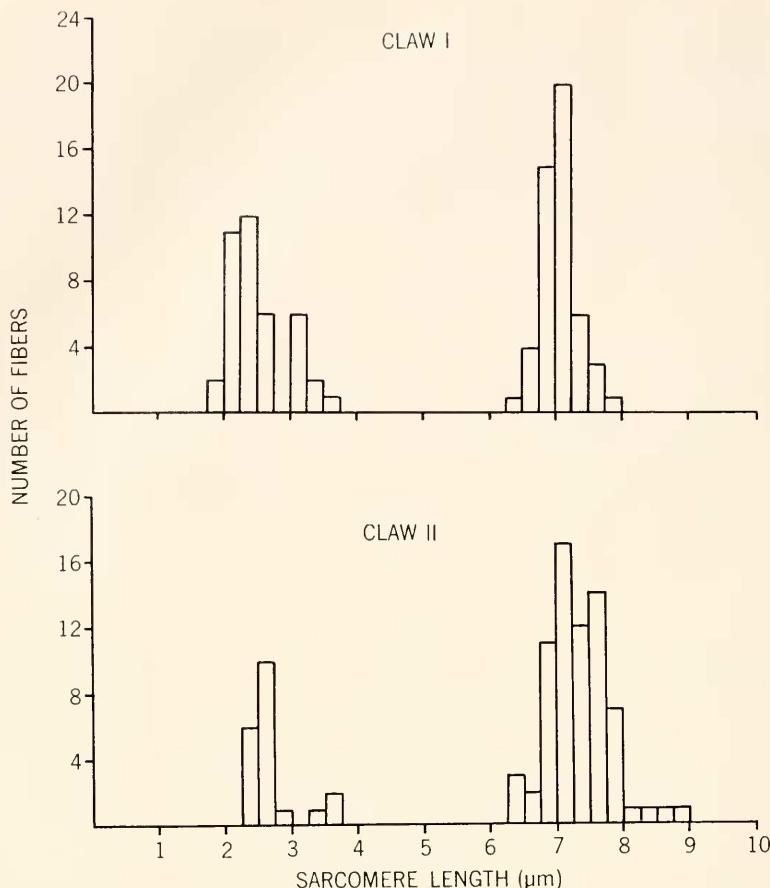


FIGURE 1. Frequency histogram of muscle fibers with characteristic sarcomere lengths from the inner aspect of the paired closer muscles of a stage 4 lobster.

muscles are characterized according to the relative distribution of short, intermediate and long sarcomere muscle fibers. As in a previous paper (Lang, Govind, and She, 1977), muscle fiber types were characterized on the basis of sarcomere lengths since we have little information regarding their physiological properties. However, other things being equal, the fibers with short sarcomeres would contract more quickly than fibers with long sarcomeres, just on the basis of having more sarcomeres in series per unit length of fiber (Jahromi and Atwood, 1969; Josephson, 1975).

In stages 4 and 5, as the paired claws cannot be separated into cutter and crusher types from external morphology, their closer muscles are labelled as Claw I and Claw II (Table I). In these cases the muscle with the higher percentage of short sarcomere fibers was regarded as belonging to Claw I. In stage 6, and subsequent stages, the paired claws are externally identifiable by their dimorphic appearance and their muscles were classified as cutter and crusher types (Table I).

Hence, for the paired muscles in Table I the dual heading Claw I/Cutter and Claw II/Crusher is used.

In most of the early juvenile stages, the closer muscle was examined at some undetermined point during the intermolt of that stage. In several animals the muscle was fixed several hours after it had molted into that stage (early) or a few hours before it might have molted into the next stage (late).

Stage 4

At the molt to stage 4 the lobster assumes its general adult form but the claws are both cutter-like in external morphology (Herrick, 1896, 1911). Except for animals newly molted to the fourth stage, each of the paired closer muscles of fourth stage lobsters is composed largely of two distinct populations of muscle fibers, namely short sarcomere ($< 4 \mu\text{m}$) and long sarcomere ($> 6 \mu\text{m}$) fibers (Table I). The bimodal distribution is clearly seen in a frequency histogram of fiber types in a stage 4 lobster (Fig. 1). The short sarcomere fibers exhibit a mode at $2.5 \mu\text{m}$ and long sarcomere fibers at $7 \mu\text{m}$; there is a distinct lack of intermediate fibers. Intermediate fibers are present, however, in the early fourth stage, where they make up approximately 10% of the population. Even this is a significant change from the third larval stage where they make up half the total fiber population (Lang, Govind, and She, 1977). Their disappearance in the early fourth stage, and its correlation with the appearance of long sarcomere fibers, will be discussed below.

It is evident that all stage 4 animals examined have closer muscles with a substantial number of short sarcomere fibers (Table I). However, in no case did they contribute less than 17% or more than 45% of the total population. In this regard, neither claw exhibits a closer muscle characteristic of the adult condition in which short sarcomere fibers constitute over 60% of the population (cutter claw) or long sarcomere fibers constitute virtually the entire population (crusher claw).

Owing to the small size of the claws in this and other early postlarval stages, it is somewhat difficult to rely on the data in regard to a possible regional distribu-

TABLE II
Regional distribution of fiber types in claw closer muscles of juvenile lobsters.

Stage	Number	Muscle fiber type based on sarcomere length (μm)											
		Dorsal area						Ventral area					
		Cutter/Claw I*			Crusher/Claw II			Cutter/Claw I			Crusher/Claw II		
		4	4-6	6	4	4-6	6	4	4-6	6	4	4-6	6
4**	4	48%	5%	47%	40%	5%	45%	15%	2%	83%	12%	12%	76%
4	3	37	3	69	49	—	51	2	—	98	1	—	99
5	2	43	2	55	58	—	42	7	—	93	3	—	97
5 (late)	1	97	—	3	37	—	63	27	7	66	3	—	97
6	4	84	—	16	22	—	78	9	1	90	—	—	100
11-13	4	99	—	1	7	—	93	23	1	76	1	1	98

* For stages 4-6, Claw I is that which has the larger percentage of fast fibers.

** Claws sampled using six regions; all others sampled with nine regions.

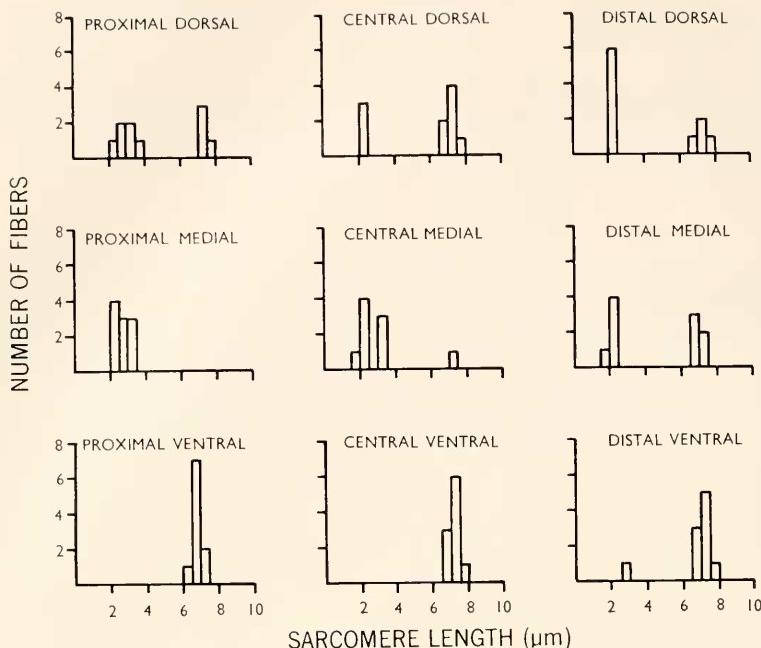


FIGURE 2. Frequency histogram of muscle fiber types (based on sarcomere lengths) showing the regional distribution pattern on the inner aspect of a Claw I closer muscle in a stage 4 lobster.

tion of fiber types. Rather, the sampling technique is meant to provide a survey of muscle fibers from all areas of the claw. In general, however, a pattern emerged that was consistent among the seven pairs of claws examined (Table II). In the ventral areas, long sarcomere fibers (sarcomeres $> 6 \mu\text{m}$) comprised 88% of all fibers sampled. In the three pairs of claws where nine areas were sampled, this distribution was even more striking. Here, where the three ventral areas consisted of the bottom one third of the muscle (as opposed to the bottom half when six areas were used), long sarcomere fibers comprised over 98% of the sample (Fig. 2). In contrast, long sarcomere fibers comprised about 50% of the sample taken in the dorsal areas for both the six and the nine region sampling technique.

Stage 5

In stage 5, the claws are still morphologically identical, but the latter part of this stage may signal the transitional period between the symmetrical claws of previous stages and asymmetrical claws of subsequent stages. In animals from early and mid-fifth stage, the muscle fibers again are largely distributed into two distinct populations of short sarcomere ($< 4 \mu\text{m}$) and long sarcomere ($> 6 \mu\text{m}$) fibers (Table I). However, both claws from each animal have fewer than 50% short sarcomere fibers; thus, there is no apparent differentiation of claw type. In fact, the claws appear essentially similar to those in fourth stage animals with the

exception of the presence of a larger proportion of fibers with sarcomere lengths in the range of 8–11 μm .

In the one animal sampled during the late fifth stage there was a striking change in the population of muscle fibers in one of the claws (Table I). Claw I of this animal contained 67% short sarcomere fibers, approximately the condition of the adult cutter claw. Given the variability of the fiber populations and the limited sample from the late fifth stage, a definitive conclusion regarding the transition of the cutter claw must await further sampling during this period of growth.

The regional distribution of fiber types within stage 5 closer muscles was similar to that observed in stage 4 animals. Ventral fibers were primarily long sarcomere (91%), while dorsal fibers were about equally divided between short and long sarcomere (Table II). Of interest, however, is the observation regarding

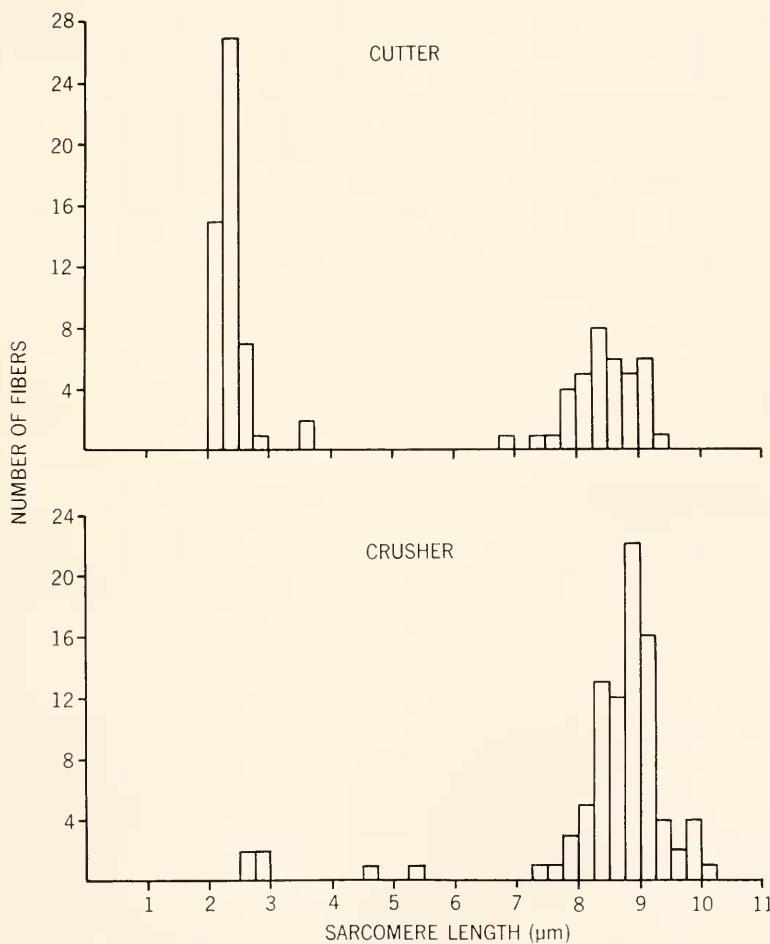


FIGURE 3. Frequency histogram of muscle fibers with characteristic sarcomere lengths from the inner aspect of cutter and crusher closer muscles of a stage 6 lobster.

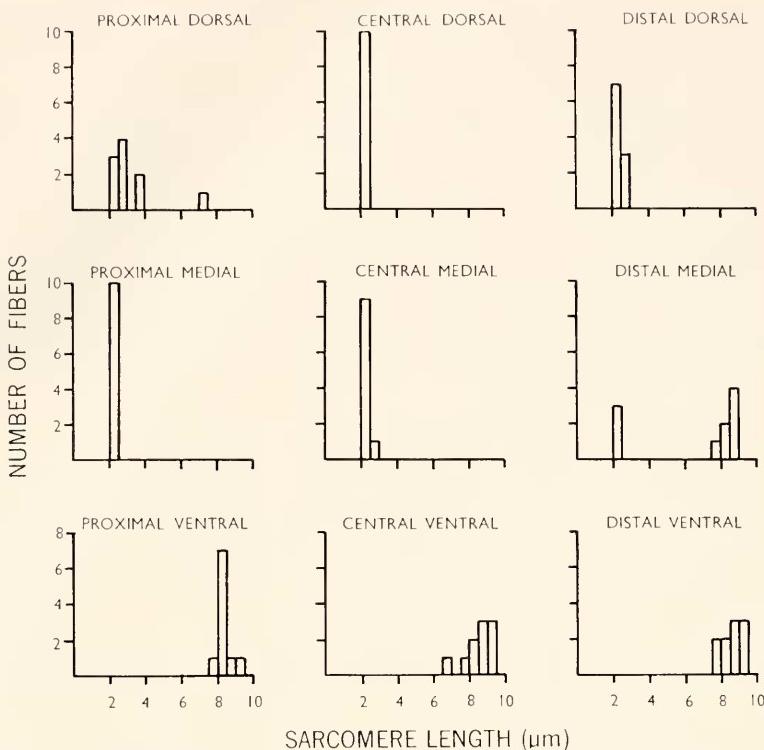


FIGURE 4. Frequency histogram of muscle fiber types (based on sarcomere lengths) showing the regional distribution pattern on the inner aspect of a cutter closer muscle in a stage 6 lobster.

the distribution of fiber types in the stage 5 animal sampled just prior to molt. In the dorsal area of the cutter claw, short sarcomere fibers now predominate, as in later stages (Table II). However, in the other claw, the presumptive crusher, there is a decrease in the relative number of short sarcomere fibers in the dorsal area.

Stage 6

During stage 6 one of the pair of closer muscles usually has a majority of short sarcomere fibers, while the other has a majority of long sarcomere fibers (Table I; Fig. 3). In addition, careful measurements of the claw at this stage revealed that the dactyl of the former was usually longer than the dactyl of the latter, an invariant characteristic of the cutter claw in all later stages. Certainly the claw with a large proportion of short sarcomere fibers in the closer muscle resembles the adult cutter claw and may therefore be regarded as having already differentiated into this form.

In one of the sixth stage animals examined, there were fewer than 50% short sarcomere muscle fibers in the putative cutter (Table I). It is uncertain whether

this represents the variability normally present in claw development or whether it merely represents sampling variability. From the available evidence, the latter seems a likely possibility. The only significant regional variation for this claw occurred in the medial region where the sample revealed equal distribution between short and long sarcomere fibers. Among the other three sixth stage cutter claws, the medial region invariably contained at least twice as many short sarcomere fibers as long sarcomere fibers (Fig. 4).

As in previous stages, the ventral regions of both claws are primarily composed of long sarcomere fibers (Table II). However, in stage 6, there is a striking change in the distribution of fibers in the dorsal regions. In the cutter claw the majority (84%) of dorsal fibers have short sarcomeres, while in the crusher claw the majority (78%) of fibers have long sarcomeres. Thus, the pattern of distribution of fiber types clearly resembles the adult pattern for the cutter claw (Lang, Costello and Govind, 1977), while that for the crusher claw is approaching the adult distribution.

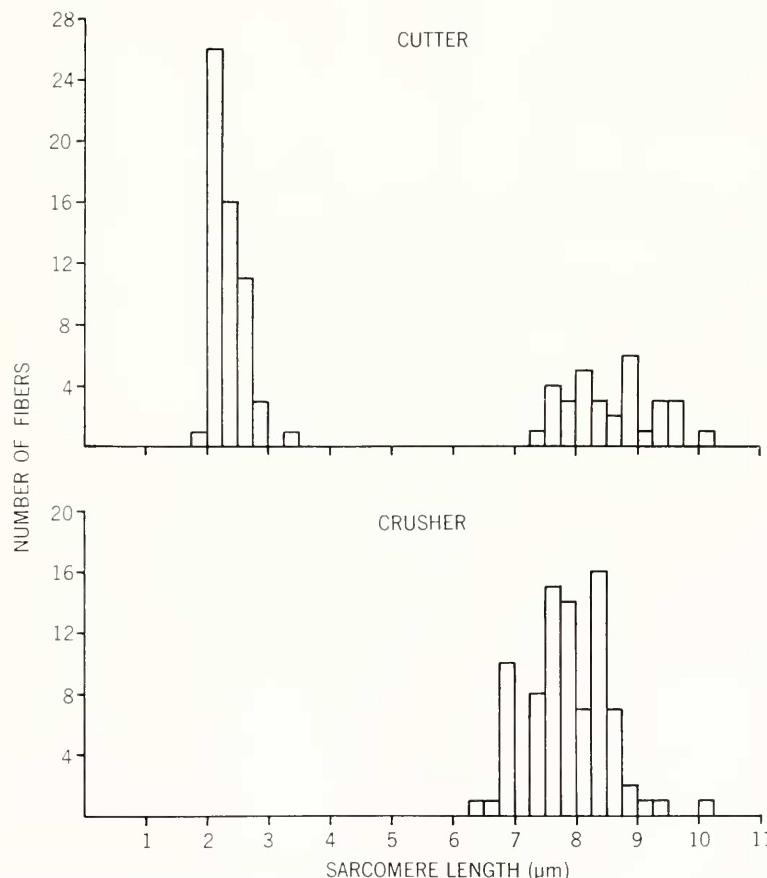


FIGURE 5. Frequency histogram of muscle fibers with characteristic sarcomere lengths from the inner aspect of cutter and crusher closer muscles of a stage 13 lobster.

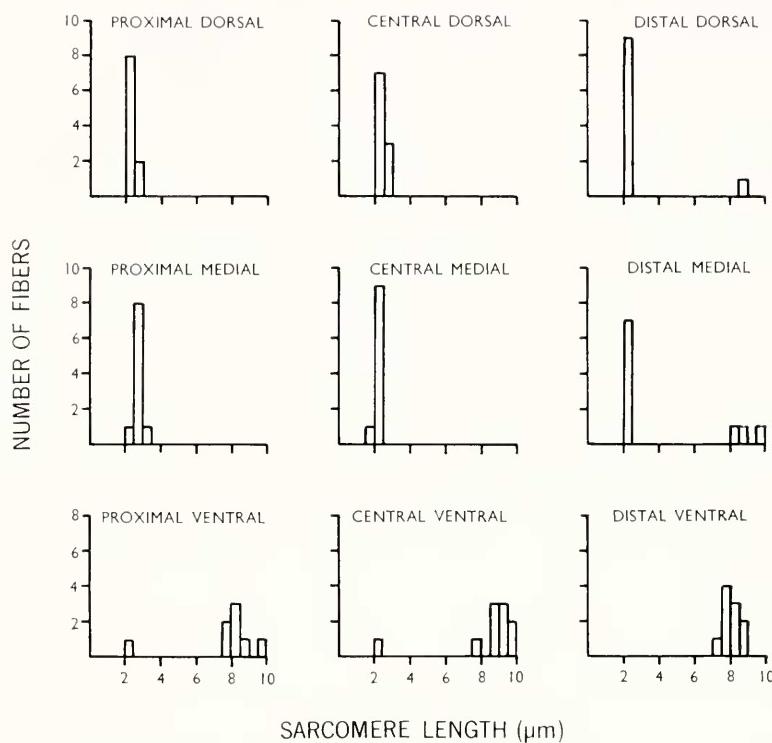


FIGURE 6. Frequency histogram of muscle fiber types (based on sarcomere lengths) showing the regional distribution pattern on the inner aspect of a cutter closer muscle in a stage 13 lobster.

Stages 11–15

The characteristic dimorphic external morphology of the claws is discernible by stage 8 or 9 and is very distinct by stage 11. At this point, the cutter claw closer muscle has assumed the adult pattern of over 60% short sarcomere fibers (Table I; Fig. 5). The crusher claw on the other hand is still in the process of completing the transformation to the adult pattern. There may be short sarcomere fibers present, even as late as stage 16 (Goudey and Lang, 1974), but these never amount to more than 35% of the total. Indeed, the number of fast fibers is usually small and in some animals they may be absent completely (Table I).

The regional distribution first manifested in stage 6 is still evident (Table II). The dorsal region of the cutter is now virtually all short sarcomere fibers (Fig. 6), while that in the crusher is composed of nearly all long sarcomere fibers. However, there has been a change in the ventral region of the cutter claw. Short sarcomere fibers now comprise 23% of the population, typical of that found in the adult (Lang, Costello and Govind, 1977).

DISCUSSION

During the larval (stages 1–3) and early postlarval (stages 4–5) period, the two claws of the lobster are identical from all external appearances, and it is not

until the sixth stage that their asymmetry is evident. The claw closer muscles follow a similar time course of change from the symmetrical to the asymmetrical condition. In larval animals, the closer muscles are very similar, each having virtually identical muscle fiber populations. The same is true in the first two postlarval stages up until the end of the fifth stage. At that time, or during the sixth stage, the transformation to the asymmetrical state occurs.

In light of the timing of the transformation of the closer muscles, it is worth reconsidering the work of Enmel (1908) on claw "reversal" in the lobster. He showed, and we have confirmed (in preparation) that claw type is not established in the fourth stage. Normally either claw has an equal probability of being a crusher or cutter. However, removal of one claw during the fourth stage will always result in the remaining claw developing into a crusher. Enmel (1908) also observed that this was true during the early fifth stage (within a day or two after molting) but not in the later part of the fifth stage or thereafter. In the latter cases, removal of a claw did not influence the remaining claw, as it would become a cutter or a crusher with equal probability. The present result at the late fifth stage correlates well with this observation. At the time when the claws have the ability to "reverse", they are essentially symmetrical. Just after the ability to reverse is lost, the muscles become asymmetrical, one assuming the characteristics of the adult cutter claw. The mechanisms responsible for the loss of reversal and the fixation of claw type are unknown but perhaps are amenable to experimental analysis.

It is of interest to note the occurrence of and changes in the regional distribution of the muscle fiber types. Previous studies on larval and adult lobster closer muscles suggested that short and long sarcomere fibers had a tendency to be prevalent in certain areas (Lang, Costello and Govind, 1977; Lang, Govind and She, 1977). In larval muscle (Lang, Govind and She, 1977) as in the fourth stage, the claws are essentially similar in the composition and location of muscle fiber types. Thus in the fourth stage, the dorsal area has an equal proportion of short and long sarcomere fibers while the ventral areas averaged over 90% long sarcomere fibers. In the sixth stage and perhaps as early as the late fifth stage, these patterns change dramatically. In the cutter claw the short sarcomere fibers increase in prevalence until they comprise virtually the entire sample from the dorsal area of stage 11–13 animals. The ventral area of the cutter exhibits little change during this growth period. On the other hand, the crusher claw muscle fibers exhibit a different pattern in the dorsal area. Here, the short sarcomere fibers present in stages 4 and 5 are replaced by long sarcomere fibers over the next 6–8 molts. The ventral fibers, which are long sarcomere fibers in stage 4, remain thus in subsequent stages.

What influences the dimorphism of the closer muscles such that short sarcomere fibers are added and long sarcomere fibers lost in the cutter muscle and *vice versa* in the crusher muscle? The two excitatory motor axons to each muscle may influence the differentiation of muscle fiber types particularly as the axons are themselves differentiated into a fast and a slow (Wiersma, 1955, 1961); the former has a larger diameter and hence a faster conduction velocity than the latter. In the cutter claw the fast axon evokes rapid (20–40 msec) closure of the claw with a single stimulus, while the slow axon causes a tonic contraction only at higher frequencies of stimulation (Wiersma, 1955; Govind and Lang, 1974). The fast and slow axons in the crusher claw are, however, "slower" versions of their

counterparts in the cutter claw so that the fast axon cannot evoke a mechanical response to single stimuli but can produce a small twitch (500 msec) to a pair of stimuli (Govind and Lang, 1974). There is, thus, some correspondence between the type of motor axons and muscle fiber composition in each closer muscle. The adult cutter closer muscle has a bimodal distribution of fast and slow muscle fibers which matches the fast and slow axons. The crusher muscle has a unimodal distribution of slow muscle fibers which matches the "slower" versions of fast and slow axons in this muscle. The differentiation of muscle fiber types may therefore be influenced by its innervating motor axon through some type of neurotrophic influence as has been demonstrated in vertebrate muscle (for reviews see Guth, 1968; Harris, 1974; Gutmann, 1976).

Considering the striking differences in morphology of the chelipeds and the physiological properties of their closer muscles, it is evident that the claws must be used for different behaviors. This is true both for the pair of claws in the adult as well as for the claws in larval and juvenile animals as compared to the adult (Lang, Govind, Costello and Greene, 1977). Thus, it would be of interest to determine the physiological properties of the motor neurons controlling the chelipeds during growth. Studies in this direction are in progress.

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SUMMARY

1. The two chelipeds of the adult lobster are asymmetrical with respect to their external morphology, neuromuscular physiology and utilization in behavior; however, they are not genetically fixed in terms of placement or handedness.

2. The differentiation of muscle fiber types was studied in the cutter and crusher claw closer muscles in the early juvenile stages of the lobster *Homarus americanus*. Muscle fibers were characterized on the basis of sarcomere length.

3. In contrast to the adult lobster, where the claw closer muscles are asymmetric, the closer muscles of the stage 4 lobster are nearly symmetric; both short and long sarcomere muscle fibers are present in each claw and both fiber types have an identical regional distribution within the closer muscle.

4. By stage 6 one of the muscles differentiates into a cutter muscle with over 60% short sarcomere fibers and a distinct regional distribution of short and long sarcomere fibers. The other claw closer muscle slowly loses its short sarcomere muscle fibers and is transformed into a crusher claw, usually by stage 13–15.

5. The change of the closer muscles from a symmetric to an asymmetric condition is correlated with the loss in ability for the claws to undergo a "reversal" rather than with the external appearance of the claw which becomes differentiated several molts later.

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